

**LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF  
*NEASPILOTA ACHILLEAE* JOHNSON (DIPTERA: TEPHRITIDAE) ON  
*STEPHANOMERIA* SPP. (ASTERACEAE) IN SOUTHERN CALIFORNIA**

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*Abstract.*—*Neaspilota achilleae* Johnson is a bivoltine fruit fly (Diptera: Tephritidae) developing solely in the flower heads of *Stephanomeria* spp. (Asteraceae) belonging to the subtribe Stephanomeriinae of the tribe Lactuceae in southern California. This species is distributed along the east coast of the United States and in California and Arizona, but has not been reported from middle America. Moreover, in the East it is reported from 17 other host-plant species in the subtribes Astereae, Hieraciinae, Lactucinae, Liatrinae, and Solidaginae of the Tribes Astereae, Eupatorieae, and Lactuceae, but not from Stephanomeriinae, which are mostly western plant species. The second- and third-instar larvae and puparium are described and figured, and these larval instars are compared with those of other *Neaspilota*. The anterior thoracic spiracle of the second instar has three papillae, but three and four papillae are reported in the third instar. The second and third instars of *N. achilleae* have an undetermined number of oral ridges with dentate posterior margins in a vertical series lateral to the oral cavity. The appearance and arrangement of these oral ridges is now known to be a distinguishing generic larval character. The numbers of these oral ridges, along with the patterns of minute acanthae circumscribing the body segments, are useful in distinguishing several species of *Neaspilota* larvae. The larvae feed mainly on the corollas of florets as first and second instars; however, as third instars, they may extend their feeding into and through the ovules or soft achenes, and sometimes into the receptacle, and supplement their diet with sap. At least two annual generations are produced in southern California. The life cycle is of the aggregative type and overwintering mainly occurs as sexually immature adults. *Pteromalus* sp. (Hymenoptera: Pteromalidae) was reared as a solitary, larval-pupal endoparasitoid of *N. achilleae*; *Eurytoma obtusiventris* Gahan or near and *E. veronia* Bugbee (Hymenoptera: Eurytomidae), as probable, solitary, larval-pupal endoparasitoids.

*Key Words:* Insecta, *Neaspilota*, *Stephanomeria*, Asteraceae, nonfrugivorous Tephritidae, biology, taxonomy of immature stages, allopatry, flower-head feeding, aggregative life cycle, seed predation, parasitoids

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Revision of the genus *Neaspilota* (Diptera: Tephritidae) by Freidberg and Mathis (1986) facilitated identification of specimens reared from California Asteraceae (Goeden 1989) and stimulated several life-history studies, including those on *N. viri-*

*descens* Quisenberry (Goeden and Headrick 1992), *N. wilsoni* Blanc and Foote (Goeden and Headrick 1999), *N. signifera* (Coquillett) (Goeden 2000a), *N. aenigma* Freidberg and Mathis (Goeden 2000b), *N. appendiculata* Freidberg and Mathis (Goeden

2000c), and *N. pubescens* Freidberg and Mathis (Goeden 2000d). This paper describes some immature stages and the life history of a seventh species from California, *N. achilleae* Johnson.

#### MATERIALS AND METHODS

The present study was based in large part on dissections of samples of flower heads of *Stephanomeria virgata* Benthams (Asteraceae) mainly collected SE of Barrett Junction at 400-m elevation, SE San Diego Co., and from *S. pauciflora* (Nuttall) Nelson mainly collected at the mouth of Big Rock Creek Canyon at 1,400 m., Angeles Nat. Forest, Los Angeles Co., during 1988 to 1997. One-liter samples of excised, immature and mature flower heads containing eggs, larvae, and puparia were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Four second- and seven third-instar larvae and six puparia dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Additional prepuparia and puparia were placed in separate, glass shell vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH and two, 1-h immersions in hexamethyldisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, and studied and photographed with a Philips XL-30 scanning electron microscope in the Institute of Geophysics and Planetary Physics, University of California, Riverside.

Most adults reared from isolated prepuparia and puparia were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper

toweling impregnated with yeast hydrolyzate and sucrose. These cages were used for studies of longevity and sexual maturation in the insectary of the Department of Entomology, University of California, Riverside, at  $25 \pm 1^\circ\text{C}$ , and 14/10 (L/D) photoperiod. Five pairs of virgin males and females obtained from emergence cages also were held in separate, clear-plastic, petri dishes provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1994) for observations of their courtship and copulation behavior.

Plant names used in this paper follow Hickman (1993) and Bremer (1994); tephritid names and adult terminology follow Foote et al. (1993). Terminology and telegraphic format used to describe the immature stages follow Goeden (2000a, b, c, d), Goeden et al. (1998), Goeden and Headrick (1992, 1999), Goeden and Teerink (1997a, b, 1998, 1999a, b), Teerink and Goeden (1999), and our earlier works cited therein. Means  $\pm$  SE are used throughout this paper. Voucher specimens of *N. achilleae* immature stages, adults, and parasitoids reside in my research collections.

#### RESULTS AND DISCUSSION

##### TAXONOMY

Adult.—*Neaspilota achilleae* was described by Johnson (1900) from several adults collected from an apparent non-host plant, *Achillea millefolium* L. (Phillips 1946). Phillips (1923) sketched the patterned wing. Benjamin (1934) provided drawings of the male antenna, wing, caudal segment in posterior view, and genitalia; female head in frontal view, wing, oviscape and aculeus. Freidberg and Mathis (1986: 28–32) redescribed this species, designated a male lectotype and three paralectotypes, and pictured the uniquely patterned wing (p. 72), along with drawings (p. 29) of the lateral aspect of the head; male right foretarsus, epandrium, distiphallus, epandrium and cerci, aculeus and its apex enlarged,

and spermatheca. Foote et al. (1993) provided a photograph of a right wing and a drawing of the fifth tarsomere of the male foreleg.

Immature stages.—Benjamin (1934) provided generalized descriptions and habit sketches of the third-instar larva and puparium as well as sketches of the anterior spiracle, caudal segments, and spiracular plate of the third instar. Phillips (1946) described the third instar and sketched its cephalopharyngeal skeleton, anterior spiracle, caudal segment in posterior view, and posterior spiracular plate and interspiracular processes. The first-instar larva remains undescribed, but the egg, second- and third-instar larvae and puparium are redescribed below with the aid of scanning electron microscopy.

*Egg*: Only three intact eggs were found and measured in situ within separate, immature, preblossom flower heads. These eggs were white, opaque, smooth, elongate-ellipsoidal, and averaged  $0.61 \pm 0.02$  (range, 0.58–0.64) mm long and  $0.16 \pm 0.00$  mm wide, tapered and smoothly rounded at both ends. As no eggs were examined by scanning electron microscopy, the egg of *N. achilleae* could only be generally compared with the eggs of *N. viridescens*, *N. wilsoni*, and *N. appendiculata*, which were described in detail by Goeden and Headrick (1992, 1999) and Goeden (2000a).

*Second instar*: White, elongate-cylindrical, rounded anteriorly, truncated posterodorsally (Fig. 1A), body segments well-defined, anterior third of meso- and metathorax circumscribed anteriorly by minute acanthae, as is anterior half of abdominal segment A-1, and all of segments A-2 through A-7 (Fig. 1D); dorsal sensory organ not well-defined, flattened (damaged in Figs. 1B-1, C-1); anterior sensory lobe (Figs. 1B-2, C) with terminal sensory organ (Figs. 1B-3, C-2), lateral sensory organ (Fig. 1C-3), supralateral sensory organ (Fig. 1C-4), and pit sensory organ (Fig. 1C-5); stomal sense organ (Figs. 1B-4, C-6)

ventrolaterad of anterior sensory lobe; mouthhook bidentate (Fig. 1B-5); median oral lobe not seen; four papilliform, integumental petals in single row dorsal to each mouthhook (Fig. 1C-7); five oral ridges seen of an unknown total, dentate along posterior margins, in vertical series lateral to oral cavity (Fig. 1B-6); prothorax, circumscribed anteriorly by posteriorly-directed, minute acanthae (Fig. 1B-7); anterior thoracic spiracle with three, doliform papillae (Fig. 1D); lateral spiracular complexes not seen; caudal segment with two stelex sensilla dorsolaterad (Fig. 1E) and ventrolaterad (Fig. 1F) of posterior spiracular plate (Fig. 1G); posterior spiracular plate bears three ovoid rimae (Fig. 1G-1), ca. 0.012 mm long, and four interspiracular processes (Fig. 1G-2), each with four, simple branches, longest measuring 0.008 mm; intermediate sensory complex (Fig. 1H) with a stelex sensillum (Fig. 1H-1) and a medusoid sensillum (Fig. 1H-2).

The habitus of the second instar of *N. achilleae* (Fig. 1A) is more like *N. wilsoni* (Goeden and Headrick 1999), *N. signifera* (Goeden 2000a), *N. aenigma* (Goeden 2000b), *N. appendiculata* (Goeden 2000c), and *N. pubescens* (Goeden 2000d) than the "barrel-shaped" (doliform) second instar of *N. viridescens* (Goeden and Headrick 1992). The dorsal sensory organ of *N. achilleae* is not well-defined in the second instar (Figs. 1B-1, C-1), like *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999), and *N. aenigma* (Goeden 2000b), but unlike *N. signifera* (Goeden 2000a), *N. appendiculata* (Goeden 2000c), and *N. pubescens* (Goeden 2000d), in which this organ is well defined. In Fig. 1B-1 and 1C-1, the cover of the dorsal sensory organ is torn away to reveal the large opening that it protects. The integumental petals of the second instars of all seven species are papilliform, but are only four in number above each mouth hook in *N. achilleae* (Fig. 1C-7), like *N. signifera* (Goeden 2000a), but are six in number in *N. viridescens* (Goeden and Headrick 1992) and *N.*





Fig. 1. Second instar of *Neaspilota achilleae*: (A) habitus, anterior to left; (B) gnathocephalon, lateral view, 1 — dorsal sensory organ, 2 — anterior sensory lobe, 3 — terminal sensory organ, 4 — stomal sense organ, 5 — mouthhook, 6 — oral ridge, 7 — minute acanthae; (C) anterior sensory lobe, 1 — dorsal sensory organ, 2 — terminal sensory organ, 3 — lateral sensory organ, 4 — supralateral sensory organ, 5 — pit sensory organ, 6 — stomal sense organ, 7 — integumental petal, 8 — oral ridge; (D) anterior thoracic spiracle; (E) dorsolateral stelex sensillum; (F) ventrolateral stelex sensillum; (G) posterior spiracular plate, 1 — rima, 2 — interspiracular process, 3 — ecdysial scar; (H) intermediate sensory complex, 1 — stelex sensillum, 2 — medusoid sensillum.

*pubescens* (Goeden 2000d), seven in *N. appendiculata* (Goeden 2000c) and *N. wilsoni* (Goeden and Headrick 1999), and eight in *N. aenigma* (Goeden 2000b). *Neaspilota achilleae* has three papillae on the anterior spiracle of the second instar (Fig. 1D), like the three or four papillae reported in second instars of *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999), *N. signifera* (Goeden 2000a), and *N. aenigma* (Goeden 2000b), but different from the five papillae in *N. pubescens* (Goeden 2000b) and eight in *N. appendiculata* (Goeden 2000c). Finally, the interspiracular processes of *N. achilleae* (Fig. 1G-2) each bear four branches, like those of *N. appendiculata* (Goeden 2000c), but not one to four branches like *N. aenigma* (Goeden 2000b) and *N. pubescens* (Goeden 2000d), nor two to four branches like *N. signifera* (Goeden 2000a), nor five to nine branches like those of *N. viridescens* (Goeden and Headrick 1992), nor two to six branches like those of *N. wilsoni* (Goeden and Headrick 1999).

*Third instar:* Pale yellow, ellipsoidal, with posterior spiracular plate dark brown to black, tapering and truncated anteriorly; posterior spiracular plate on caudal segment flattened and upturned dorsally ca. 60° (Fig. 2A), minute acanthae circumscribe anterior fifth of meso- and metathorax, anterior fourth of first abdominal segment, but all of remaining abdominal segments, except for pleura of segments, A6 and A7; gnathocephalon conical (Fig. 2B); dorsal sensory organ defined by a crescentic fold (Fig. 2B-1), attached dorsally (Fig. 2C-1) and punctured centrally and peripherally by pores (Fig. 2C-2); anterior sensory lobe (Fig. 2C) bears terminal sensory organ (Fig. 2C-3), lateral sensory organ (Fig. 2C-4), supralateral sensory organ (Fig. 2C-5), and pit sensory organ (Fig. 2C-6); eight, papilliform (upper row) or spatulate (lower row), integumental petals in two rows above each mouthhook (Figs. 2C-7, D-1); at least six oral ridges (Figs. 2B-2, D-2), at least five toothed ventrally, and all lateral to oral cav-

ity; stomal sense organ (Figs. 2C-8, D-3) ventrolaterad of anterior sensory lobe; mouthhook (Figs. 2B-3, D-4) tridentate; median oral lobe laterally flattened, (Figs. 2B-4, D-5); prothorax circumscribed by minute acanthae (Fig. 2B-5); verruciform sensilla circumscribe prothorax anteriorad of minute acanthae (Fig. 2B-6); anterior thoracic spiracle on posterior margin of prothorax bears three or four oblong papillae (Fig. 2E); mesothoracic lateral spiracular complex with a spiracle (not shown) and six verruciform sensilla (Fig. 2F-1), one above and five below the spiracle; metathoracic lateral spiracular complex with a spiracle (Fig. 2F-2) and five verruciform sensilla (Fig. 2F-3), one above and four below the spiracle; lateral spiracular complexes of abdominal segments A-1 and A-2 each with a spiracle (Fig. 2G-1) and six verruciform sensilla (Fig. 2G-2), one dorsoposteriorad of the spiracle, another posteriorad of the spiracle, one pair ventroposteriorad of the spiracle aligned longitudinally, and another ventral pair aligned ventrally; a stelex sensillum dorsolaterad, laterad, and ventrolaterad (not shown) of posterior spiracular plate (not shown); each posterior spiracular plate bears three ovoid rimae, ca. 0.03 mm in length, and four interspiracular processes, each with four, simple or forked, pointed branches, longest branch measuring 0.013 mm; intermediate sensory complex (Fig. 2H) with a stelex sensillum (Fig. 2H-1) and a medusoid sensillum (Fig. 2H-2).

The habitus of the third instar of *N. achilleae* is like that reported for *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999), *N. signifera* (Goeden 2000a), and *N. aenigma* (Goeden 2000b), *N. appendiculata* (Goeden 2000c) and *N. pubescens* (Goeden 2000d). The pattern of the minute acanthae that circumscribe the body segments is unique for *N. achilleae* in that the acanthae, which uniquely appear to occur in individual depressions, increase their coverage posteriorly from the anterior fifths of the thoracic segments to include nearly all of the ab-

dominal segments beyond the first; whereas, in *N. signifera* (Goeden 2000a), *N. appendiculata* (Goeden 2000c) and *N. pubescens* (Goeden 2000d), the anterior part of each body segment is circumscribed, in *N. aenigma* the anteriors, pleura, and posteriors of each segment are circumscribed (Goeden 2000b); in *N. wilsoni*, all intersegmental areas and all abdominal segments except the pleura are circumscribed (Goeden and Headrick 1999); and in *N. viridescens*, the intersegmental areas are free of acanthae (Goeden and Headrick 1992). Like *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999) and *N. pubescens* (Goeden 2000d), but unlike *N. signifera* (Goeden 2000a), *N. aenigma* (Goeden 2000b) and *N. appendiculata* (Goeden 2000c), the dorsal sensory organ is not well-defined and flattened, and not dome-shaped, in the third instar of *N. achilleae* (Fig. 2C-1).

Additional similarities involved the integumental petals in the third instars of all six congeners examined to date, all of which are arranged in a double row above each mouthhook and papilliform (upper row) or spatulate (lower row) (Goeden and Headrick 1992, 1999; Goeden 2000a, b, c, d). The integumental petals differ in number among species and generally increase in number between the last two instars. The stomal sense organ of the third instar of *N. achilleae* bears one pair each of campaniform and short papilliform (conical) sensilla (Figs. 2C-8, D-3); therefore, it appears slightly less complex than the stomal sense organ of the second instar, which bears at least six sensilla (Figs. 1B-4, C-6). However, the stomal sense organs of the third instars of the five other congeneric species examined appear more complex than earlier instars and each bears different combinations of sensory structures, variously described as several cone-shaped sensilla in *N. viridescens* (Goeden and Headrick 1992); as papilliform and pit-type in *N. wilsoni* (Goeden and Headrick 1999); as verruciform or "compound verruciform" in *N.*

*signifera* (Goeden 2000a), as verruciform and pit-type in *N. aenigma* (Goeden 2000b), and as verruciform, pit-type, and cone-shaped or short papilliform in *N. pubescens* (Goeden 2000d).

The third instars of all seven species of *Neaspilota* examined to date have oral ridges with dentate ventral margins characteristically arranged in vertical series ventro-laterad of the dorsal sensory organ and laterad of the oral cavity (Goeden and Headrick 1992, 1999; Goeden 2000a, b, c, d; Figs. 2B-2, D-2). Though unfortunately partly hidden and not counted in *N. achilleae* (Figs. 2B-2, D-2), the oral ridges number eight in *N. pubescens* (Goeden 2000d), seven or eight in the third instar of *N. aenigma* (Goeden 2000b), seven in *N. appendiculata* (Goeden 2000c), but six in the second and third instars of the other three congeners examined to date. The dentate margins and vertical, parallel arrangement of these oral ridges appears to be a generic character; however, Goeden (2000c, d) confirmed that the oral ridges vary in number among third instars of some *Neaspilota* species. Also, the most ventral, eighth oral ridge of *N. pubescens* is not ventrally toothed (Goeden 2000d). The third instars of *Trupanea imperfecta* (Coquillett), *T. jonesi* Curran, *T. nigricornis* (Coquillett), *T. pseudovicina* (Hering), *T. signata* Foote, and *T. wheeleri* Curran also bear serrated oral ridges (Goeden and Teerink 1997b, 1998, 1999a; Goeden et al. 1998; Knio et al. 1996; Teerink and Goeden 1999), but these oral ridges appear to be fewer in number, and are not arranged in a more or less regular, vertical row laterad to the mouth hook, as in *Neaspilota*.

The mouthhooks of the third instars of *N. appendiculata*, *N. aenigma*, *N. signifera*, *N. viridescens*, and *N. achilleae*, and probably *N. pubescens*, are tridentate (Goeden and Headrick 1992; Goeden 2000a, b, c; Goeden 2000d; Figs. 2B-3, D-4); whereas, those of the third instar of *N. wilsoni* are bidentate (Goeden and Headrick 1999). Such interspecific differences in dentation



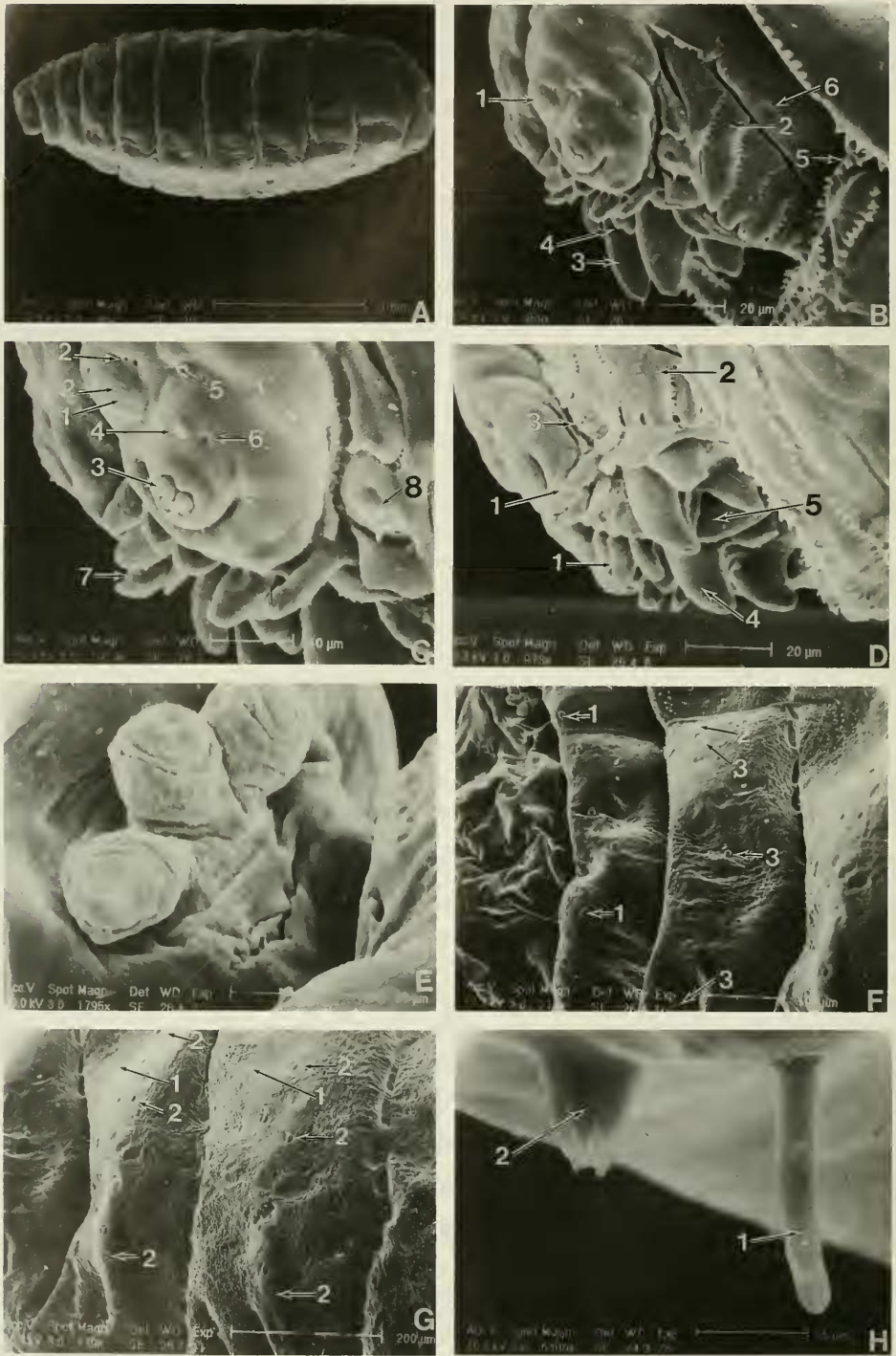


Fig. 2. Third instar of *Neaspilota achilleae*: (A) habitus, anterior to left; (B) gnathocephalon, lateral view, 1 — dorsal sensory organ, 2 — oral ridge, 3 — mouthhook, 4 — median oral lobe, 5 — minute acanthae, 6 — verruciform sensillum; (C) anterior sensory lobe, 1 — dorsal sensory organ, 2 — pores, 3 — terminal sensory organ, 4 — lateral sensory organ, 5 — supralateral sensory organ, 6 — pit sensory organ, 7 — integumental petal, 8 — stomal sense organ; (D) oral cavity, ventrolateral view, 1 — integumental petals, 2 — oral ridge, 3

are supported by our findings that the mouthhooks of third-instar *Trupanea vicina* (Wulp) are bidentate; whereas, those of 12 other congeners examined from California are tridentate (Goeden and Teerink 2000b and citations therein).

Phillips (1946) described and illustrated the anterior spiracle of what I presume was the third instar as having three papillae; whereas, three and four papillae were reported by Benjamin (1934), as also reported for the anterior spiracles of my specimens (Fig. 2E). Moreover, the interspiracular processes of eastern U.S. specimens were described and illustrated by Phillips (1946) as being six to 12 in number, lanceolate, and almost never branched; whereas, my specimens had interspiracular processes each of which were four-branched (or four in number in Phillips terminology), pointed and simple (lanceolate) or forked. These results indicate morphological differences in eastern and western U.S. specimens of third instars of *N. achilleae* (see discussion below on distribution).

The number and appearance of the stelex sensilla surrounding the posterior spiracular plate differ among the *Neaspilota* species examined to date. These number only four in the first instars of *N. wilsoni* (Goeden and Headrick 1999), *N. aenigma* (Goeden 2000b), and *N. appendiculata* (Goeden 2000c), but, unfortunately, were not observed with *N. signifera* (Goeden 2000a) or in the present study. This count of stelex sensilla remains at four in the second instars of *N. aenigma* (Goeden 2000b) *N. appendiculata* (Goeden 2000c), *N. pubescens* (Goeden 2000d), and *N. achilleae* (Fig. 1E, F), and increases to six in third instars of *N. wilsoni* (Goeden and Headrick 1999), *N. aenigma* (Goeden 2000b), *N. appendiculata*

(Goeden 2000c), and *N. achilleae*. These stelex sensilla also show inter-instar (intra-specific) and interspecific differences in the incidence and appearance of the minute acanthae that may ring them basally, but this was not recognized, studied or recorded by my coworkers and me until recently (Goeden 2000b, c, d). The stelex sensilla of the second instar of *N. achilleae* are surrounded by four to seven, conical, minute acanthae (Figs. 1E, F); however, these stelex sensilla lack such basal minute acanthae in the third instar.

*Puparium*: Dirty white to light brown, transversely ringed with narrow, brown or black lines, posterior two or three segments brown to black, ellipsoidal, and smoothly rounded at both ends (Fig. 3A); anterior end bears the invagination scar (Fig. 3B-1) and anterior thoracic spiracles (Fig. 3B-2); caudal segment circumscribed by minute acanthae; three stelex sensilla, dorsolaterad, laterad, and ventrolaterad of posterior spiracular plates; posterior spiracular plate bears three broadly elliptical rimae (Fig. 4C-1), and four interspiracular processes, each with four, simple or forked, apically pointed branches (Fig. 4C-2); intermediate sensory complex with a medusoid sensillum and a stelex sensillum. Thirty-nine puparia averaged  $2.65 \pm 0.04$  (range, 2.07–2.99) mm in length;  $1.14 \pm 0.015$  (range, 0.92–1.30) mm in width.

#### DISTRIBUTION AND HOSTS

Freidberg and Mathis (1986) described the distribution of *N. achilleae* as, "Eastern and Gulf coast of North America from Newfoundland to Alabama and southwestern United States, southern California and Arizona." They and Foote et al. (1993) both mapped the distribution to include

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— stomal sense organ, 4 — mouthhook, 5 — median oral lobe; (E) anterior thoracic spiracle; (F) meso- (left) and metathoracic (right) lateral spiracular complexes, 1 — verruciform sensilla on mesothorax, 2 — spiracle and 3 — verruciform sensilla on metathorax; (G) lateral spiracular complexes of first (left) and second (right) abdominal segments, 1 — spiracle, 2 — verruciform sensilla; (H) intermediate sensory complex, 1 — stelex sensillum, 2 — medusoid sensillum.



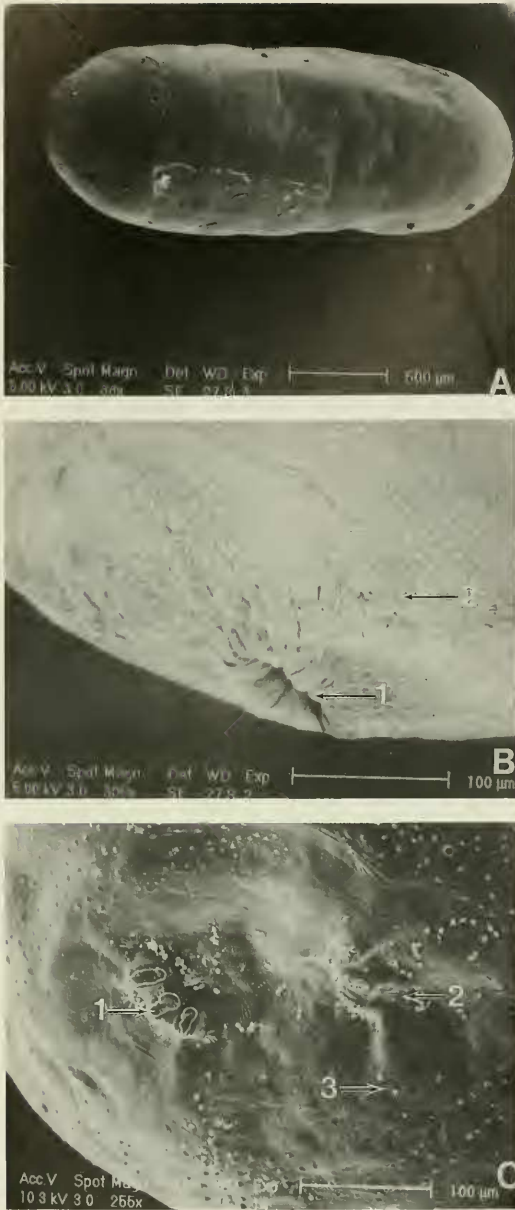


Fig. 3. Puparium of *Neaspilota achilleae*: (A) habitus, anterior to left; (B) anterior end, 1 — invagination scar, 2 — anterior thoracic spiracle; (C) caudal segment, 1 — rima, 2 — interspiracular process, 3 — intermediate sensory complex.

only a single location in Arizona. Freidberg and Mathis (1986, p. 32) also remarked that:

“The known distribution of *N. achilleae* is peculiar. It is apparently widespread and com-

mon and has been reared from several host plants from numerous sites along the east coast. However, several specimens have also been examined from California and Arizona. The latter specimens are smaller on the average than their eastern counterparts, but otherwise they seem to be conspecific. Further collecting and rearing will be necessary to determine whether the distribution of this species is disjunct or if the species actually extends across southern United States.”

Goeden (1989) discussed the host plants of *N. achilleae* and noted that Freidberg and Mathis (1986) listed four species of *Aster*, three species of *Chrysopsis*, three species of *Hieraceum*, and one species each of *Prenanthes*, *Sericocarpus*, and *Trilisa* as hosts of *N. achilleae* in eastern United States. Updating Goeden (1989), I note that I have reared other genera and species of *Neaspilota*, but never *N. achilleae*, from totals of 50 samples of mature flower heads of 10 species of *Aster*, 17 samples of three species of *Chrysopsis*, 43 samples of 10 species of *Erigeron*, five samples of two species of *Hieraceum* from California. On the other hand, I have not reared *N. achilleae* from one sample of *Stephanomeria cichoriacea* Gray, eight samples of *S. exigua* Nuttall, nor two samples of *S. parryi* Gray. My host record for *S. pauciflora* (see above) is new. Eastern host plants belong to the subtribes Asterinae, Hieraciinae, Lactucinae, Liatrinae, and Solidaginae of the tribes Astereae, Eupatorieae, and Lactuceae, but include no other Stephanomeriinae which primarily are western plant species (Bremer 1994). However, eastern and western *N. achilleae* do share hosts in the Lactucinae (Bremer 1994). Thus, in southern California, *N. achilleae* appears to be nearly monophagous; whereas, in the eastern U.S., it is a generalist (Headrick and Goeden 1998).

#### BIOLOGY

Egg.—In each of seven, closed, preblossom, immature flower heads of *S. pauciflora* a single egg of *N. achilleae* was inserted pedicel-last; six of these eggs were placed

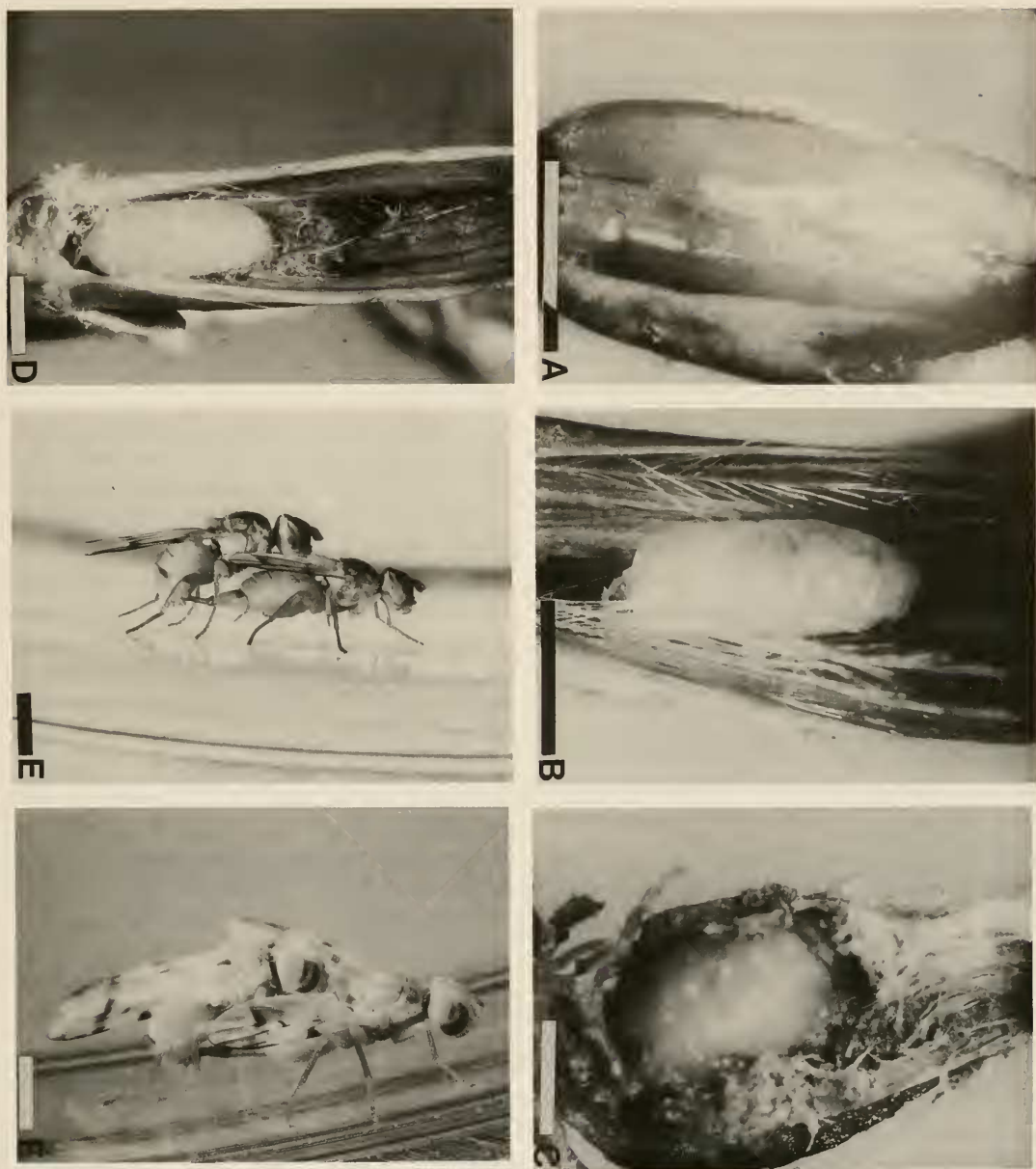


Fig. 4. Life stages of *Neaspilota achilleae* in *Stephanomeria pauciflora* (Figs. A, B, D) and *S. virgata* (Fig. C): (A) egg between ovules in closed, preblossom flower head, (B) early-third instar, (C) late-third instar, (D) newly formed puparium, (E) mating adults, lateral view, (F) mating adults, dorsolateral view. Lines = 1 mm.

between an inner phyllary and a peripheral floret with their long axes parallel to the long axes of the flower heads (Fig. 4A). The seventh egg had been inserted through the phyllaries and was embedded for half its length in the corolla of a peripheral floret.

Larva.—Upon eclosion, the seven first instars found feeding in separate, preblossom flower heads either tunneled into an ovule, or into a corolla before entering the ovule to which the corolla was basally attached. The receptacles averaged  $0.87 \pm 0.08$  (range, 0.57–1.12) mm in diameter and

an average of  $1.3 \pm 0.19$  (range, 1–2) florets/ovules was damaged in these seven flower heads. No receptacle was abraded or pitted by larval feeding. Based on  $5 \pm 0.07$  (range, 3–6) as the average total number of florets, ovules or achenes respectively counted in 45 preblossom to postblossom flower heads, about  $26 \pm 3.7\%$  (range, 20–40%) of the ovules in the seven flower heads were damaged by first instars.

Second instars continued feeding on corollas or ovules in preblossom flower heads. All fed with their bodies more or less perpendicular to and their mouthparts directed towards or away from the receptacles, but always well above the receptacles. Receptacles of three flower heads containing second instars averaged  $0.84 \pm 0.05$  (range, 0.75–0.93) mm in diameter. These flower heads each contained a single larva that had damaged an average of  $3 \pm 1$  (range, 2–5) florets/ovules, or about 60% (range, 40–100%) of the average total of 5 ovules per flower head.

Third instars (Fig. 4B) initially continued to feed mainly on ovules and soft achenes in preblossom, blossom, or postblossom flower heads. Seventy-one flower heads that averaged  $1.06 \pm 0.06$  (range, 0.56–3.13) mm in diameter each contained a single third instar or puparium. An average of  $5.0 \pm 0.09$  (range, 3–6) of the soft achenes therein were damaged, or 100% of the average total of 5 ovules/soft achenes per flower head (Fig. 4C). These percentages of seed predation per larva per flower head, like those reported for *N. aenigma* (Goeden 2000b), *N. appendiculata* (Goeden 2000c), and *N. pubescens* (Goeden 2000d), are higher than other florivorous tephritids studied by us to date (Headrick and Goeden 1998). For *N. achilleae*, this higher percentage results from the small-size flower heads of the host plants attacked in southern California and small number of ovules/achenes contained in each flower head (Fig. 4C). Higher percentage seed destruction per flower head also was evidenced by gregarious florivorous species like *Trupanea conjuncta* (Adams) (Goeden

1987) and *T. pseudovicina* Hering (Goeden and Teerink 1998) or by species with large larvae that develop in immature or small flower heads like *Paracantha cultaris* (Coquillett) (Cavender and Goeden 1982) and *Xenochaeta dichromata* Snow (Goeden and Teerink 1997a). Also, the rate of flower head infestation per sample for *N. achilleae* was very low, e.g., a mean of 2.9% (range, 1%–6%) for seven subsamples of 200 to 400 dissected flower heads, similar to most other *Neaspilota* that we have studied (unpublished data).

Third instars in flower heads fed with their long axes oriented perpendicular to and mouthparts directed towards the receptacles (Fig. 4C). Only seven (10%) of the third instars in the 71 infested heads containing thirds instars or puparia scored or pitted the receptacles; however, most larvae presumably supplemented their diet with sap. Goeden and Headrick (1992, 1999) and Goeden (2000c, d) described and discussed this type of feeding by *N. viridescens*, *N. wilsoni*, *N. appendiculata*, and *N. pubescens*, respectively. Upon completing feeding, the larvae oriented with their anterior ends away from the receptacles, retracted their mouthparts, and formed prepuparia (Headrick and Goeden 1998). Most individuals pupariated (Fig. 4D) and emerged in summer (July–August) and either produced at least one additional generation in the same, long-blooming host-plant species or in its alternate host plants growing at higher elevations.

Adult.—Adults are long-lived in nature. Under insectary conditions, 17 unmated males averaged  $69 \pm 10$  (range, 11–139) days, and 11 virgin females averaged  $30 \pm 6$  (range, 11–75) days. Such lengthy longevities for males compare favorably with average adult longevities reported for adults of *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999), *N. signifera* (Goeden 2000a), *N. aenigma* (Goeden 2000b), *N. appendiculata* (Goeden 2000c), and *N. pubescens* (Goeden 2000d). The shorter average longevities re-



corded for females of *N. achilleae* are unexplained.

The pre mating and mating behaviors of *N. achilleae* were not studied in the field, but were observed in petri dish arenas found to be so useful with many other non-frugivorous, tephritid species (Headrick and Goeden 1994). Premating behaviors observed with paired *N. achilleae* were abdominal pleural distension and side-stepping by males while tracking females (Headrick and Goeden 1994) and rapid wing hamation, sometimes combined with lofting about 20° by both sexes (Headrick and Goeden 1994). No trophallaxis or nuptial gift presentation was noted as reported with *N. viridescens* (Goeden and Headrick 1992). Six matings, two by one pair during a 2-week period (Figs. 4E, F) were observed, most of which began during late afternoon at dusk and lasted an average of  $153 \pm 54$  (range, 80–420) min (or 2 h and 33 min on average). Except for the single pair that began mating at 08:00 h and remained *in copula* for 420 min (7 h), this average was shorter than the average durations of 190 min reported for *N. aenigma* (Goeden 1999b), 235 min reported for *N. wilsoni* (Goeden and Headrick 1999), 238 min reported for *N. signifera* (Goeden 2000a), 285 min reported for *N. appendiculata* (Goeden 2000c), 318 min reported for *N. viridescens* (Goeden and Headrick 1992), and 1032 min reported for *N. pubescens* (Goeden 2000d).

All matings were observed only after copulation had begun, suggesting that precopulatory behavior was perfunctory. The mating position (Fig. 4E, F) was such that the wings of the male were parted from about 5 to 30°, while the wings of the female were parted at about 30 to 80°, with both pairs of wings centered over their respective body midlines. The body of the female was held parallel to the substrate, while the body of the male was elevated about 20° anteriorly (Fig. 4E). The hind- and midtarsi of the male usually rested on the substrate (Figs. 4E, F), but sometimes

his midtarsi grasped the base of the aculeus, while his foretarsi hooked over the anterior abdominal terga of the female (Figs. 4E, F). The male's mouthparts were positioned above syntergite 1 + 2 of the female (Figs. 4E, F). The pair largely remained quiescent with only their mouthparts pumping, or sometimes both formed regurgitation droplets (Headrick and Goeden 1994). Besides tightly clinging to the female, the male would sometimes reposition his foretarsi so as to gain better purchase or rub his midtarsi alternately along her oviscape to induce passivity as a variation on copulatory induction behavior (Headrick and Goeden 1994). These bursts of activity as the female kicked at the male and arched her body in an attempt to dislodge the male always preceded disengagement, but only infrequently resulted in disengagement; similar behavior also was reported for *N. pubescens* (Goeden 2000d).

A single mating termination and disengagement was observed, which involved the male turning in place and walking away from the female while pulling his phallus from within her, however, this process took 34 sec as the male had difficulty freeing himself. Disengagement by *N. pubescens* (Goeden 2000d) was reported to last less than 10 s. Postcopulatory behavior by *N. achilleae* mainly consisted of storing of the genitalia by males and cleaning and grooming by both sexes (Headrick and Goeden 1994).

Seasonal history.—The life cycle of *N. achilleae* in southern California follows an aggregative pattern (Headrick and Goeden 1994, 1998) in which the adult is the principal overwintering stage. Come late spring (May), overwintered adults aggregate on preblossom shoots of *S. pauciflora* to mate and oviposit in the small, newly-formed, closed, preblossom flower heads beginning in June. The F<sub>1</sub> larvae feed until fully grown, then pupariate in flower heads and emerge as adults in summer (July–August) to produce another generation at higher elevations on *S. pauciflora* or on *S. virgata*

that flower through September–October. There are at least two generations per year, with  $F_2$  adults emerging in October–November to overwinter as long-lived adults in reproductive diapause. *Neaspilota signifera* (Goeden 2000a) and *N. aenigma* (Goeden 2000b) also overwinter principally as adults in southern California.

Natural enemies.—A male and a female of *Pteromalus* sp. (Hymenoptera: Pteromalidae) were reared from separate puparia of *N. achilleae* as solitary, larval-pupal endoparasitoids. One female each of *Eurytoma obtusiventrus* Gahan or near and *E. veronia* Bugbee (Hymenoptera: Eurytomidae) were reared from separate flower heads of *S. virgata* and *S. pauciflora*, respectively, as probable, solitary, larval-pupal endoparasitoids.

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